The role of nutrients in temperate and tropical freshwater may differ since Deevey (1957) has noted that the nitrogen-phosphorus ratios (N/P) were lower in Central American lakes than in temperate waters by a factor of as great as five. He suggested that nitrogen deficiency may be general in the tropics. These relationships imply that eutrophication problems also may vary in temperate and tropical waters. Since eutrophication can result from an increase in the absolute concentration of N and P and shift in the N/P ratio can amplify the process, we might expect in tropical lakes that an addition of sewage could not only increase the concentration of N and P but also change their ratio. This supposition is not supported by study of Lake Amatitlán where the N increased by a factor of six but phosphorus remained constant (Weiss, 1971b). Even so, there has been a four- to sevenfold increase in production in Lake Amatitlán. Clearly these nutrient processes require detailed study under tropical conditions.

Brylinsky and Mann (1973) used multiple regression and factorial analysis for data collected from widely ranging latitudinal zones as part of an International Biological Program study. When all latitudes were considered, they found that solar energy input had a greater influence on production than nutrient concentration. However, for lakes within a narrow range of latitude, nutrient-related variables became more important in influencing primary production. These comparative studies are extremely important since they suggest the limits to community process we can expect under normal environmental conditions. In this sense they form a baseline against which change in the aquatic system can be measured. Clearly many more studies of this type are needed.

3. River systems

The principal river systems of the tropics, including the prominent Amazon, Congo, Nile, and Mekong Rivers, are of immense unrealized biological significance. Due to their close relationship with the economic growth of the regions they occupy, these rivers will undoubtedly be changed markedly within the next few decades. Whatever information is lost in the transition of these systems to a postindustrial state will be an unfortunate handicap to tropical ecological investigation and may well hinder effective management of the associated resources.

The volume and drainage area of the major tropical rivers is large and forms a habitat complex unlike any temperate counterpart. The flow of the Amazon is eight times and the Congo two times that of the Mississippi (Sioli, 1964). The mainstem of these river systems, although impressive in volume and biotic diversity, constitutes only a small portion of the environmental complex derived from runoff in tropical regions. Tributary rivers and streams determine water chemistry of the mainstem and support a significant biota of their own. Such habitats are ecologically unknown except in certain restricted

regions in South Africa and the Amazon. Valuable but scattered studies of the smaller rivers and streams are cited in a review by Hynes (1970).

Some unique communities are associated with tropical rivers and the relative importance of various community types may differ greatly from the temperate zone. One striking example is provided by the enormous mats of floating vegetation or "floating meadows" (Marlier, 1962; Sioli, 1968; Junk, 1970). Backwaters and waterbodies within the flood plain such as the várzea lakes of the Amazon (Sioli, 1968; Schmidt, 1969) are also important environmental components of tropical river systems, especially since the floodplain has frequently not been altered by man. Direct economic importance of the backwaters and várzea lakes is probably great because they may supply the nursery requirements for commercially important fishes (W. Junk, personal communication).

Few biological or physicochemical generalizations can be made regarding lotic environments of the tropics. This is due partly to ignorance and partly to the great range of conditions prevailing in these environments. The humid tropics contribute the vast majority of flow, but many major rivers traverse or receive seasonal contributions from arid regions. Very dilute rivers are frequently found in the lowland humid tropics. The Orinoco, for example, carries only about 50 ppm TDS (Livingston, 1963). Low dissolved-solids content of many lowland tropical rivers is due in part to efficient absorption and retention of salts by organic material in the watersheds. Parent material and relief also account for wide variation in tributary composition in the largest river systems. Sioli (1963, 1964) distinguishes the "white" water of the lower Amazon, which receives its sediment load from areas of high relief, from both the "clear" waters such as the Rio Tapajos and the "black" waters such as the Rio Negro, which flow from areas of low relief. The black waters of the Rio Negro are acid (pH 3.8 to 4.9), low in electrolytes (Ca < 5 mg/1, Mg < 0.4 mg/1, HCO_3 < 0.04 m val/1) and high in humic colloids and humic acid, which give the brown color to the water and reduce the light needed for photosynthesis. Biological production in the water is therefore very low (Sioli, 1954, 1955, 1963, 1965a, b). Janzen (unpublished, 1973) finds evidence that the humic materials may also be toxic to some organisms.

Sioli (1963, 1964) has also recognized the role of bedrock in producing runoff of varied composition within the Amazon basin. As would be expected, specific regions of the tropics have peculiarities that are reflected in their rivers and streams. The waters of East Africa, for example, are remarkably low in sulfate (Beauchamp, 1953). The great range of variation in African surface waters is documented by the work of Talling and Talling (1965). Higher level of silicates in tropical freshwaters, predicted by Hutchinson (1957) on the basis of early data and the higher mobility of silicate under alkaline conditions, has recently been verified by Talling and Talling (1965) in Africa and Kobayashi (1966) and Lewis (1973b) in Southeast Asia. They demonstrated the presence of high silicate concentrations even when other plant nutrients were scarce. Community composition and adaptive features can obviously be affected by such factors. More generalizations of this type can be expected due to the fundamental differences between tropical and temperate weathering processes.

Terrestrial studies have shown that in the lowland tropics standing crop provides large nutrient pools due to the low ratios of productivity to biomass of the mature tropical terrestrial ecosystems. As the mean age of these ecosystems is rapidly lowered by man, one might reasonably expect a radical change in chemical composition of the more dilute tropical waters and a concurrent change in biota.

Variations in the biota of rivers can be largely understood in terms of chemical composition, rate of flow, and turbidity. Most tropical rivers, like those of the temperate zone, can be expected to show seasonal variation in volume of flow, hence seasonal variation in chemical composition and turbidity. Kobayashi's (1959) study of river chemistry in Thailand has demonstrated tropical seasonality particularly well, and Prowse and Talling (1958) have documented seasonal variation of the Nile plankton.

Other climatic and biotic factors influence tropical rivers but their effect may be more difficult to judge *a priori*. Tropical rivers are distinct from temperate-zone rivers in relative seasonal uniformity of temperature and insolation, although mean temperatures can be consistently very low at high altitudes. Biological functions and interactions may well be affected by this uniformity in ways that are unique to the tropics.

Zoogeographical accidents are another principal source of contrast between temperate and tropical running water. The rivers of North America, for example, are dominated by cyprinid, catastomid, ictalurid, and to a lesser extent centrarchid and percid fishes. The Amazon, by contrast, supports a high diversity of characin and siluriform fishes that contribute to a total fauna of nearly 2,000 species (Darlington, 1957). Large African rivers are comparably diverse in fish fauna, but have distinctive dominant groups such as the mormyrid fish. Whether the organization of food webs in tropical rivers is radically different due to the special adaptive capabilities of the top trophic levels in the various major river systems is not known. The origin of and ecological support for high diversity within the top trophic levels of tropical rivers also await explanation.

The large tropical river systems are without doubt the greatest habitat frontier in modern aquatic ecology. Study of these systems would not only increase our general knowledge of freshwater ecology, both in a descriptive and a conceptual sense, but would provide important data for planning a rational pattern of resource use.